Cost of seed versus rhizome production in *Agropyron repens*

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I examined growth and allocation patterns in genotypes of *Agropyron repens* isolated from six habitats that differed in disturbance frequency. The trade-off between seed and rhizome production and between either mode of propagation and growth of leaves, stems, and roots was determined by calculating both within- and among-genotype correlations between functions. I also examined how level of light and nitrogen availability affected these trade-offs. Large differences were found among populations in how resources were divided between infructescences and rhizomes, but there was no evidence of a direct trade-off. Regardless of environment, or level at which correlations were examined, there was never a negative correlation between seed and rhizome production. Depending on level of nitrogen and light availability, there was usually a trade-off between seed or rhizome production and growth of leaves, stems, and roots. The two modes of propagation differed in how they responded to resource availability such that their relative cost varied among environments. I suggest differences among populations in allocation to seed versus rhizome production are due to these differences in cost. When cost of seed production is high relative to rhizome production, allocation to rhizome is favored. Conversely, when cost of rhizome production is high relative to seed production, allocation to infructescences is favored.

Key words: vegetative reproduction, sexual reproduction, allocation, disturbance, reproductive cost, resource availability, clonal growth.

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L'auteur a examiné la croissance et les patrons d'allocation chez les génotypes de l'*Agropyron repens* isolés à partir de six habitats qui diffèrent entre eux par la fréquence des dérangements. La répartition entre production des graines, production des rhizomes, entre les modes de propagation, la croissance des feuilles, des tiges et des racines ont été déterminés en calculant à la fois les corrélations existant à l'intérieur et entre les génotypes pour les différentes fonctions. Il a aussi examiné comment l'intensité lumineuse et la disponibilité de l'azote affectent ces répartitions. Il a trouvé une grande différence entre les populations, quant à la façon avec laquelle les ressources sont divisées entre les infructescences et les rhizomes, mais n'a pas trouvé d'évidence pour une répartition directe. Indépendamment de l'environnement ou du niveau auquel les corrélations ont été examinées, il n'a jamais pu trouvé de corrélations négatives entre la production des graines et celle des rhizomes. Dépendant du niveau de la teneur en azote et de la lumière disponible, il y a habituellement une répartition entre la production des graines et des rhizomes et la croissance des feuilles, des tiges et des racines. Les deux modes de propagation diffèrent en ce qu'ils réagissent à la disponibilité des ressources de telle façon que leurs coûts relatifs varient selon les milieux. L'auteur suggère que les différences entre les populations quant à l'allocation aux graines versus aux rhizomes sont dues à ces différences dans les coûts. Lorsque le coût de la production des semences est relativement élevé par rapport à la production des rhizomes, la location du rhizome est favorisée. Réciproquement, quand les coûts de production du rhizome sont élevés comparativement à la production de graines, l'allocation favorise les infructescences.

Mots clés : reproduction végétative, reproduction sexuelle, allocation, dérangement, coût de reproduction, disponibilité des ressources, croissance clonale.

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Introduction

There has been considerable interest in how resources are divided between seed production and vegetative propagation in clonal organisms (Willson 1983; Armstrong 1984; Bazzaz et al. 1987; McCrea and Abrahamson 1987; Lovett Doust 1989). Several different theories have been proposed to explain variation in allocation between these two modes of propagation (e.g., Abrahamson 1975; Sackville Hamilton et al. 1987). These theories assume that there is a trade-off between the two functions, and that allocation between them is controlled by the relative success of seedlings versus vegetative ramets. Evidence for the assumed trade-off is based on inverse correlations between reproductive allocation and allocation to structures involved in clonal growth (e.g., rhizomes and stolons). However, not all studies find this inverse correlation. In asters, for example, reproductive allocation and rhizome allocation are positively correlated (Ashmun et al. 1985).

Some recent studies of the effect of seed production on growth suggest that the cost of reproduction is highly variable and in some circumstances negligible. Antonovics (1980) used photoperiod manipulations to control level of reproduction in *Plantago lanceolata* and found that vegetative growth was only reduced at high levels of reproduction. Jurik (1985) used a model of carbon balance to examine the cost of vegetative versus sexual propagules in *Fragaria*. He found that cost per propagule was lowest in open habitats and greatest in closed habitats. Reekie and Bazzaz (1987*a*, 1987*b*) examined the trade-off between seed production and growth in *Agropyron repens* by controlling reproduction with photoperiod manipulations. The effect of reproduction on growth varied with genotype and environment, and in some cases reproduction had no effect on growth, or even enhanced growth. Horvitz and Schemske (1988) experimentally produced plants of *Calathea ovandensis* differing in level of reproductive output by removal of young inflorescences. No difference was found in the subsequent survival, growth, and reproduction of these two groups.

The fact that costs of both seed production and clonal propagation may vary suggests a novel explanation for differences among plants in allocation between modes of propagation. Assuming that the cost of seed production varies independently

from that of clonal propagation, it can be argued that allocation to seed production should increase when the cost of seed production is low relative to the cost of vegetative propagation. Conversely, allocation to vegetative propagation should increase when its cost is low relative to that of seed production. This explanation is based on the premise that plants minimize the overall cost of propagation by preferentially allocating resources to the mode of propagation that minimizes the detrimental effects of propagation upon growth.

In this paper I examine the relative importance of seed production and clonal propagation among populations of *Agropyron repens* adapted to different disturbance regimes. This species is a weedy, perennial grass that can propagate by seed or radial spread of its rhizomes. Tripathi and Harper (1973) compared numbers of seeds and rhizome buds produced by this species with seeds produced by a related nonclonal species, *Agropyron canium*. Total number of seeds and buds produced by the two species did not differ, suggesting a direct trade-off between reproduction and clonal growth. Here I determine if there is a trade-off between these two functions at the intraspecific level and to what extent allocation to these two modes of propagation affects growth of leaves, stems, and roots. These trade-offs were examined at various levels of light and nitrogen availability to determine to what extent the cost of seed versus rhizome production may vary with environment. Costs were also partitioned into within- and among-genotype components, as it has been shown that environmental costs may differ from genetic costs (Primack and Antonovics 1982). I had four major objectives: (*i*) examine the relative importance of seed versus rhizome production among populations subjected to varying degrees of disturbance; (*ii*) determine the nature and extent of the trade-off between seed and rhizome production and between either mode of propagation and growth; (*iii*) determine if the trade-off functions were constant or varied with resource availability; and (*iv*) if the trade-offs do vary, determine whether differences in allocation patterns among populations can be interpreted in terms of these changing trade-offs.

Materials and methods

Description of sites

Plant material was collected from three locations in central Saskatchewan, Canada. Each location represented a different farm, but all were managed by the University of Saskatchewan College of Agriculture. At each location there were two adjacent sites: one annual cropland and one perennial grassland. Cropland sites were subjected to a series of crop–fallow rotations, usually consisting of 2 years of small grains (most commonly wheat) followed by a fallow year. Grassland sites consisted of mixtures of perennial grasses of which *A. repens* was an important component but differed in age (i.e., time since soil was last disturbed by cultivation). The youngest site was the Goodale site (6 years), followed by the Kernan site (ca. 20 years), and then the Termunde site (ca. 35 years). Management practices varied from year to year but were limited to grazing by cattle or mowing for hay. None of the three grassland sites was heavily utilized, and all exhibited a substantial amount of biomass aboveground over the course of the growing season. Further details concerning these six sites can be found in Table 1.

Experiment 1

Rhizome material was collected from six individual plants at each site. Individual plants were always at least 10 m apart and isolated from other individuals of *A. repens* and, therefore, probably represent different genotypes. Single-node rhizome fragments from each plant

TABLE 1. Comparison of the six sites from which plant material was collected

	Goodale		Kernan		Termunde	
	GC	GG	KC	KG	TC	TG
Latitude	52°03′N		52°09′N		51°52′N	
Longitude	106°31′W		106°32′W		104°52′W	
Soil association	Bradwell		Bradwell and Sutherland		Biggar	
Soil texture	Mixed sandy loam to clay loam		Mixed clay, clay loam, and loam		Mixed gravelly loam and sandy loam	
Topography	Gently to moderately rolling		Undulating		Mixed undulating and rolling areas	
Management	Small grain production	Hay field	Small grain production	Unmanaged at present but used for pasture and hay in the past	Small grain production	Hay field at present but used as pasture in the past
Associated species	*Triticum aestivum*	*Elymus canadensis*, *Medicago sativa*	*Triticum aestivum*	*Bromus inermis*	*Triticum aestivum*	*Agropyron desertorum*
Time since last cultivation (years)	0	6	0	20	0	35

NOTE: Sites were located on three different farms and at each farm there were paired cropland and grassland sites. Site names were abbreviated as follows: GC, Goodale cropland; GG, Goodale grassland; KC, Kernan cropland; KG, Kernan grassland; TC, Termunde cropland; TG, Termunde grassland.

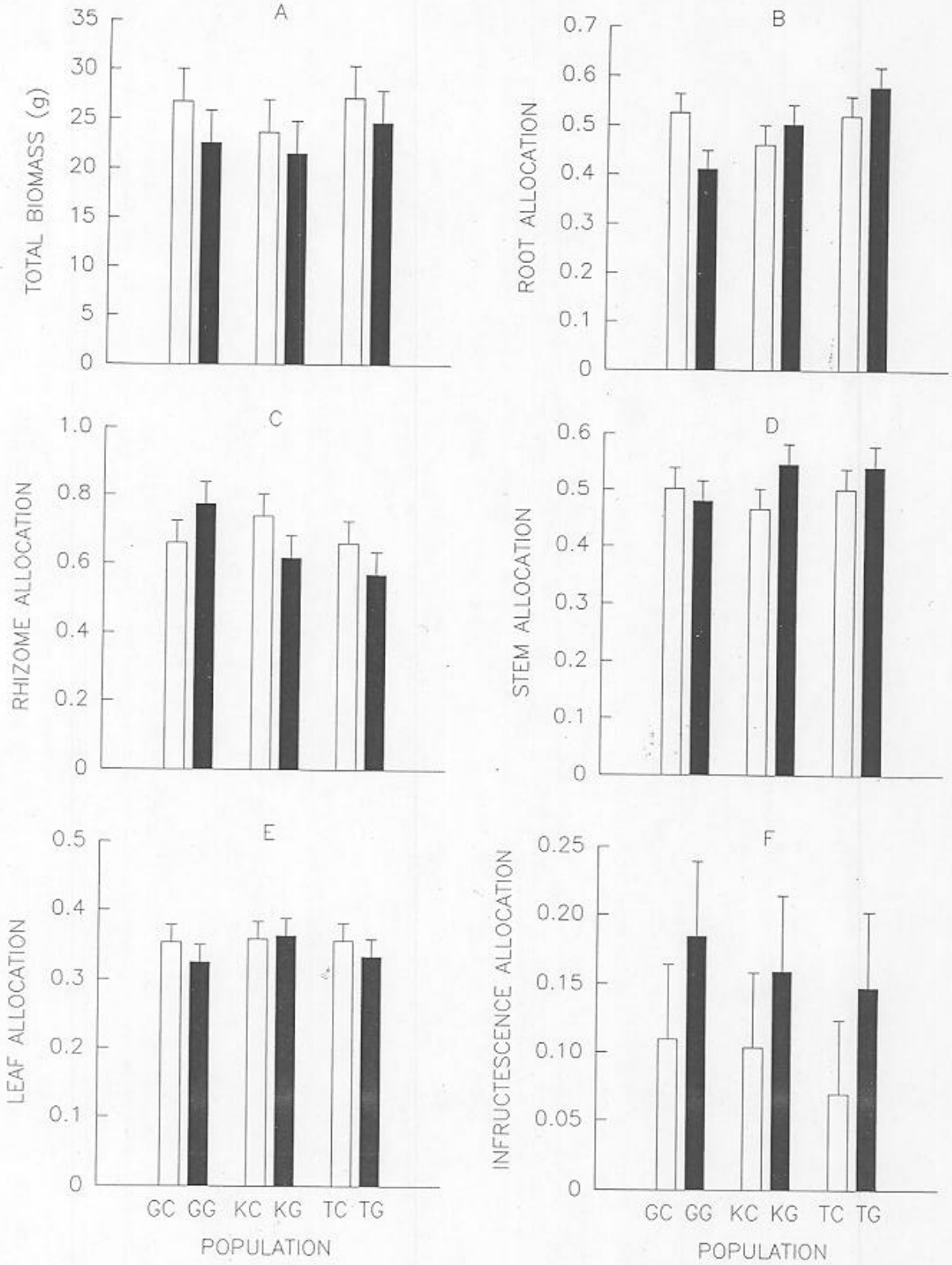

FIG. 1. Growth and allocation patterns in genotypes of *Agropyron repens* isolated from sites that experienced different disturbance regimes. (A) total biomass. (B) Root allocation. (C) Rhizome allocation. (D) Stem allocation. (E) Leaf allocation. (F) Infructescence allocation. All allocation parameters represent the arc sine transformed values. Error bars represent the 95% confidence interval for a single treatment mean. GC, Goodale cropland; GG, Goodale grassland; KC, Kernan cropland; KG, Kernan grassland; TC, Termunde cropland; TG, Termunde grassland.

TABLE 2. Trade-off between vegetative propagation and sexual reproduction and between mode of propagation and either overall growth or growth of leaves, stems, and roots combined in experiment 1

	Total biomass		Biomass of leaves, stems, and roots		Infructescence biomass	Rhizome biomass
	Rhizome allocation	Infructescence allocation	Rhizome allocation	Infructescence allocation	Rhizome allocation	Infructescence allocation
Overall	−0.16	0.08	−0.65***	0.02	−0.10	−0.01
Among genotypes	−0.32	−0.09	−0.78***	−0.06	−0.18	−0.20
Within genotypes	0.06	0.32**	−0.41***	0.17	0.05	0.28*

NOTE: Trade-offs were quantified by calculating the correlation between proportional allocation to either rhizomes or infructescences and biomass of the remaining structures. Overall phenotypic correlations were partioned into among- and within-genotype components by nested analysis of covariance.
*Significant at 0.05.
**Significant at 0.01.
***Significant at 0.001.

were grown in pots in a greenhouse for a period of 9 months. At that time three 3-cm single-node rhizome fragments were isolated from each plant and planted in 14 cm diameter pots containing 1 L of a sterilized 1:1 mixture of sand and loam. Pots were placed in a growth chamber, which provided a photosynthetic photon flux density of 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Temperature and day-length conditions were varied over the course of a 4-month period to approximate conditions of a normal growing season. Initial light:dark temperature was 15:10°C and was changed at monthly intervals to 20:15, 25:20, and 20:15°C. The initial photopoerid was 15 h and was changed at 2-week intervals to 16, 17, 18, 18, 17, 16, and 15 h. Pots were watered as needed and fertilized at weekly intervals for the first 8 weeks using Peters® soluble fertilizer (12 N–31 P–14 K). Air movement within the chamber was vigorous, ensuring adequate pollen transfer among genotypes; all plants that flowered set seed. This species is largely self-incompatible, and seed set in the field is often poor owing to limited intermixing of genotypes (Werner and Rioux 1977). Plants were harvested at the end of the 4-month period. Plants were divided into infructescences (i.e., fruiting structures), stems, leaves, roots, and rhizomes, and the material was dried at 50°C until there was no further loss in weight.

Data were analyzed using the NESTED procedure of SAS (version 6 for personal computers). The experimental design was completely random with replications (clones) of each genotype nested within genotype and genotypes nested within populations. Differences among populations were tested for by a priori pairwsie *t*-tests using the genotype effect as the error term. To assess the trade-off between seed and rhizome production and between either mode of propagation and growth, a correlative technique was used (Primack and Antonovics 1982). I determined the correlations between proportion of biomass allocated to infructescences or rhizomes and (*i*) infructescence or rhizome biomass, (*ii*) biomass of leaves, stems, and roots combined, and (*iii*) total plant biomass. Overall phenotypic correlations were broken down into among- and within-genotype components using a nested analysis of covariance with replications nested within genotypes. All proportional data were transformed prior to statistical analysis using the arc sine transformation.

Experiment 2

This experiment involved growing five replications of three genotypes at two levels of light and two levels of nitrogen availability in a completely crossed factorial treatment design. Plants were propagated from single-node rhizome cuttings as described above. Plants were grown in plastic pots 12 cm in diameter containing 1 L of Turface®. Turface is an inorganic medium (frittered clay) containing only trace amounts of nutrients. The pots were placed in a controlled environment chamber programmed to provide a constant air temperature of 25°C, a relative humidity of 75%, and an 18-h photoperiod. Nutrients were supplied by watering with Evans' modified Shive solution (Salisbury and Ross 1978) at 3-day intervals. High-nitrogen plants received the amount of nitrogen available in a full-strength Evans' solution. Low-nitrogen plants received one-fifth the nitrogen received by high-nitrogen plants. Level of nitrogen availability was manipulated by changing the concentration of $Ca(NO_3)_2$ in the nutrient solution. The level of calcium was maintained at the level in a full-strength Evans' solution by the addition of $CaCl_2$. Plants in the low- and high-light treatments received 480 and 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively. The low-light level was achieved by constructing shade-cloth canopies in the growth chambers. The experiment was terminated when the majority of plants had flowered and set seedss (77 days). Plants were separated into leaves, stems, infructescences, rhizomes, and roots and oven-dried at 50°C to a constant weight.

The trade-off between reproduction and clonal growth was assessed as described above by means of nested analysis of covariance. Separate analyses were conducted for each of the four combinations of light and nitrogen. In each of the above analyses, individuals were nested within genotypes. Only within-genotype correlations are reported here. Because of the small number of genotypes in this experiment (three), among-genotype correlations may not be meaningful. The different genotpyes were included to increase the scope of inference and to ensure adequate pollination.

Results

The populations did not differ in total weight (Fig. 1A) nor were there any differences among genotypes within populations in total weight ($p < 0.0978$). However, there were marked differences in allocation patterns among populations (Fig. 1). There was an increase in proportion of biomass allocated to roots from the youngest grassland site (GG) to the oldest site (TG). The cropland sites were intermediate between the youngest and oldest grassland sites and as a result GC > GG, KC = KG, and TG > TC. Plants from the youngest grassland site (GG) allocated a larger proportion of biomass to rhizomes than the oldest grassland site (TG). The medium-aged site (KG) was similar to TG and less than GG in this respect. The three cropland sites did not differ in allocation to rhizomes and were again intermediate between the youngest and oldest grassland sites. The youngest grassland site (GG) allocated less biomass to stems than either KG or TG and was not significantly different from any of the cropland sites in this attribute. There were no differences in stem allocation among cropland sites. There were no differences among populations in proportion of biomass allocated to leaves. Allocation to infructescences was greater in grassland populations than in cropland ones.

Regardless of whether correlations were examined at the overall phenotypic level, among genotypes, or within geno-

TABLE 3. Trade-off between vegetative propagation and sexual reproduction and between mode of propagation and either overall growth or growth of leaves, stems, and roots combined, as affected by resource availability

Resource state	Total biomass		Biomass of leaves, stems, and roots		Infructescence biomass	Rhizome biomass
	Rhizome allocation	Infructescence allocation	Rhizome allocation	Infructescence allocation	Rhizome allocation	Infructescence allocation
LN, HL	−0.62*	0.18	−0.73**	0.19	−0.36	−0.32
LN, HL	−0.81***	−0.38	−0.92***	−0.51	0.20	0.59*
HN, LL	0.35	−0.26	−0.04	−0.35	−0.11	−0.13
HN, HL	−0.65*	−0.71**	−0.81**	−0.70**	−0.20	−0.26

NOTE: Plants were grown at either low (LN) or high (HN) nitrogen and either low (LL) or high (HL) light. Trade-offs were quantified by calculating the within-genotype correlation between proportional allocation to either rhizomes or infructescences and biomass of the remaining structures.
*Significant at 0.05.
**Significant at 0.01.
***Significant at 0.001.

types, no significant negative correlation was found between proportional allocation to rhizomes and either overall growth of biomass of infructescences in experiment 1 (Table 2). However, there was a negative correlation between rhizome allocation and the summed biomass of leaves, stems, and roots. Allocation to infructescences was not negatively correlated with any other aspect of plant growth, including total biomass, rhizome biomass, or the summed biomass of leaves, stems, and roots. At the within-genotype level, there were actually positive correlations with total biomass and rhizome biomass.

The results of experiment 2 demonstrate that the trade-offs between functions varied depending on resource availability (Table 3). At low levels of available nitrogen, there were significant negative correlations between rhizome allocation and both total biomass and biomass of leaves, stems, and roots. At high nitrogen, these negative correlations disappeared completely or decreased in magnitude. Increases in light availability enhanced, rather than reduced, the negative correlations between rhizome allocation and growth. Light and nitrogen availability also affected the trade-off between infructescence allocation and biomass of leaves, stems, and roots; it was only with the combination of high light and high nitrogen that there was a significant negative correlation. The only significant correlation between modes of propagation was a weak positive correlation between rhizome biomass and infructescence allocation in the low-nitrogen high-light environment.

Discussion

Marked differences were found among populations in allocation to infructescences versus rhizomes (Fig. 1). Recent studies have shown that differences among plants in allocation to reproduction (Sampson and Werk 1986; Weiner 1988) or to clonal propagation (Hartnett 1990) may be a function of plant size. Plants often display predictable changes in allocation patterns with variation in size. Size-dependent allocation patterns are thought to be the result of morphological constraints. The differences among populations in allocation patterns in the present study, however, were not the result of size dependencies. In spite of the extensive variation in allocation patterns, there were no significant differences among populations, or among genotypes within populations, in plant size.

Abrahamson (1975) has suggested that in clonal organisms, allocation to reproduction should increase at the expense of clonal growth with increases in density. At low densities, increased allocation to clonal growth facilitates rapid spread with low risk. At higher densities, local conditions for growth are unfavourable owing to resource depletion, and reproduction allows dispersal and colonization of new sites. If the cropland sites are taken to be low-density sites and the grassland sites are taken to be high-density sites, the results of the present study are, to an extent, in accord with the above prediction. Proportion of biomass allocated to infructescences was higher, and the proportion of biomass allocated to rhizomes was generally lower, in grassland populations than in cropland populations (Fig. 1). The GG population was anomalous, however, in that the highest allocation to both rhizomes and infructescences. As a grassland population one would expect it to have a high allocation to seed production, but it is difficult to explain its high rhizome allocation. It should also be noted that in spite of its high allocation to both modes of propagation, total growth was similar to that of other populations (Fig. 1).

Implicit in the Abrahamson hypothesis, as well as in more general explanations of the balance between reproduction and clonal growth (Sackville Hamilton et al. 1987), is the assumption that the two modes of propagation are alternatives. Increased allocation to one mode of propagation results in a proportional decrease in the other, the balance being determined by the relative success (i.e., survivorship) of the two types of propagules. It follows that there should be a negative correlation between reproduction and clonal growth. No evidence of a direct trade-off between seed and rhizome production could be found in *Agropyron repens*. This was true whether correlations were examined at the phenotypic level, among genotypes, or within genotypes (Table 2) and regardless of environment (Table 3). However, there was a cost associated with infructescence and rhizome allocation. This cost is reflected in the negative correlations with the growth of leaves, stems, and roots. These costs varied depending on resource availability.

The fact that nitrogen and light availability differentially affected the cost of infructescence versus rhizome allocation (Table 3) can explain the differences in allocation patterns among populations (Fig. 1). A major difference between grassland and cropland sites in this region is the much lower nitrogen availability in long-term grassland sites (Coupland et al. 1974). Cultivation stimulates the decomposition of organic matter in the soil, which releases substantial amounts of nitrate (Paul 1976). Cropland and grassland sites also differ in light availability. During the early part of the growing sea-

son, and over the entire course of a fallow year, the ground surface of cropland sites is exposed to full sunlight. In contrast, less than 15% of full sunlight reaches the ground surface under a well-developed grass canopy in this region (Ripley and Redmann 1980).

Given these differences in light and nitrogen availability, differences among populations in allocation to infructescences versus rhizomes can be interpreted in terms of the effect of resource availability on costs of the two alternatives. Cropland populations may allocate less to infructescences than grassland populations (Fig. 1) because cost of infructescence allocation is greater in a high-light, high-nitrogen environment (Table 3). On the other hand, the decrease in allocation to vegetative reproduction from the youngest grassland site to the oldest (Fig. 1) may reflect the increase in cost of rhizome allocation as nitrogen levels decrease (Table 3). The youngest grassland site, because of its recent history of cultivation, would have larger amounts of available nitrogen than the older grassland sites. The young grassland site also had a high proportion of the legume, *Medicago sativa*, in the community (Table 1), which would further increase the amount of available nitrogen through nitrogen fixation. Cropland populations also experience high-nitrogen availability and might be expected to allocate a large proportion of their resources to rhizomes. The comparatively low allocation of cropland populations to rhizomes, however, can be explained by the high-light availability in these sites. Increased light availability increased the cost of rhizome allocation (Table 2).

The strength of the above explanation is that it can account for plants that have a high allocation to both rhizomes and infructescences with no adverse effects on growth. The GG population, for example, had the highest allocation to both rhizomes and infructescences, while total biomass was similar to that of other populations. This type of strategy is possible providing costs of both infructescence and rhizome allocation are low. Current explanations of the division of resources between reproduction and clonal growth assume a constant trade-off between the two activities and cannot explain this result.

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